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THE EARLY STAGES OF THE FAMILIES TRICHOCERIDAE AND ANISOPODIDAE (= RHYPHIDAE) (DIPTERA: NEMATOCERA)

By Prof. D. Keilin, F.R.S., and P. Tate.

(*From the Molteno Institute, University of Cambridge.*)

(Communicated by Dr. F. W. Edwards, F.R.S.)

With Eighty-seven Figures in the Text.

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I. Introduction.

In recent years study of the early stages of Nematocera has yielded results which have often caused systematists to modify greatly the systematic position assigned to genera or families on the basis of adult characters only. This is especially true of the families Tipulidae, Anisopodidae and Mycetophilidae. On adult characters the genus *Mycetobia* was placed by most entomologists in the family Mycetophilidae, although Dufour (1849), Perris (1870) and Osten-Sacken (1892) had all emphasised the close resemblance between the larvae of *Mycetobia* and *Rhyphus* (*Anisopus*). Further study of the early stages by Keilin (published in 1919) led Edwards (1916) to reinvestigate the adult structure

of the MYCETOPHILIDAE and the RHYPHIDAE (ANISOPODIDAE), from which he concluded that: "The genus *Mycetobia* (and with it *Mesochria*, though not *Ditomyia* or *Symmerus*) must therefore, on grounds of adult as well as larval structure, be transferred from the MYCETOPHILIDAE to the RHYPHIDAE." Later Edwards (1928), from a general consideration of the adults and of the early stages as described by Keilin in the same paper, decided that the genera *Anisopus* (= *Rhyphus*) and *Mycetobia* should be placed together in the family ANISOPODIDAE, which also contains the genera *Lobogaster*, *Olbiogaster* and *Mesochria*.

Again, the genus *Trichocera* was placed in the tribe Limnophilini of the TIPULIDAE, but from a study of the early stages Keilin (1912) decided that the larva of *Trichocera* is a typical eucephalous larva and, as it also differs from all Tipulid larvae in other characters, it should be separated from the TIPULIDAE. He considered that while the eucephalous nematocerous larvae were not sufficiently well known to decide the matter with certainty, there was a striking resemblance between the larval heads of *Trichocera* and *Rhyphus fenestralis*. Alexander (1919, 1920) placed *Trichocera* in a special sub-family, TRICHOCERINAE, of the family RHYPHIDAE. As regards the adult characters, however, Edwards (1923 : 475) gave the opinion that "even if the study of the early stages has shown that this is not a true Tipulid, and is in many respects similar to *Anisopus*, it still seems open to question whether it should be included in the same family." More recently Edwards (1928 : 2) concluded, with regard to *Trichocera*, that: "In this case however the writer has been unable to discover anything which suggests confirmation of the view of Alexander and some others that *Trichocera* should be included in the ANISOPODIDAE. In almost every respect the adults of this genus are typical Tipulids, but the larvae being so very different it seems necessary to regard the genus as forming a separate family." Edwards accordingly erected the family TRICHOCERIDAE for the genus *Trichocera*, remarking that: "It seems probable that we should regard *Trichocera* as a primitive genus which in its larvae at least has retained many of the characters of the ancestors of the TIPULIDAE, and its resemblances to the ANISOPODIDAE are probably due to this fact." In a recent paper Edwards (1938 : 152) maintained the opinion that *Trichocera* should not be placed in either the TIPULIDAE or the ANISOPODIDAE (RHYPHIDAE) but should be placed in a separate family because: "It is as impossible to ignore the similarities of the adult *Trichocera* to the TIPULIDAE as it is to pass over the resemblance of the larvae to the RHYPHIDAE, consequently it is now agreed that the most satisfactory course is to treat the TRICHOCERIDAE as forming a separate family."

In the paper by Edwards (1928) mentioned above one of us (Keilin, 1928) gave a brief description of the main points in the biology and morphology of the early stages of the genera *Mycetobia*, *Anisopus*, *Olbiogaster* and *Mesochria* of the ANISOPODIDAE, and of *Trichocera*. In the present paper it is intended to extend and complete the descriptions of the early stages of these genera as far as the material available permits, and to endeavour, from this comparative study, to obtain some indication as to the relationships of these genera to each other and to other Nematocera.

II. TRICHOCERIDAE.

The early literature on the genus *Trichocera* has been reviewed by Keilin (1912) when describing the larval stages, and by Edwards (1928) so that it is unnecessary to deal with it again here.

The *Trichocera*, or " Winter gnats," are widely distributed throughout the world and are common in all temperate regions. They derive the popular name of " Winter gnat " from their being most frequent during the late autumn, winter and spring months, when, during suitable weather conditions, the swarms of dancing males are a familiar sight. Apparently the females usually remain in sheltered resting-places and do not take part in the dancing, but if a female enters a swarm of males, pairing takes place at once (Edwards, 1928).

The larvae live among dead and decaying leaves and in other decaying vegetable matter such as rotting root vegetables, fungi, decomposing wood or garden refuse. They are most readily found in potatoes, turnips and, especially, mangold-wurzels, which have partly decayed when stored in " pits " for the winter. *Trichocera* larvae are usually found associated with larvae of *Scatopse*, *Sapromyza*, STRATIOMYIIDAE and *Lonchaea*.

1. Larva of *Trichocera hiemalis* De Geer.

The fully grown larva is about 8–9 mm. long and is composed of a head capsule, 3 thoracic and 8 abdominal segments (fig. 1). Superficial folds divide each of the thoracic segments into two, and each of the abdominal segments into three, parts. The integument is yellowish and is covered with small cuticular setae amongst which there are a number of long, flat, tapering sensory setae. On the ventral surface of each of the 3 thoracic segments there are two groups of hairs in connection with the imaginal discs of the legs. Each group consists of four hairs, two long and two short, and they represent the sensory vestiges of the legs (fig. 9). The last abdominal segment terminates in 4 fleshy lobes, between which the postabdominal spiracles are placed (fig. 6). The fleshy lobes are arranged in two pairs, a pair of small dorsal lobes and a pair of larger ventral ones. They all have a plate of thickened cuticle on the inner surface and are fringed with long setae. The anus opens ventrally on the last abdominal segment.

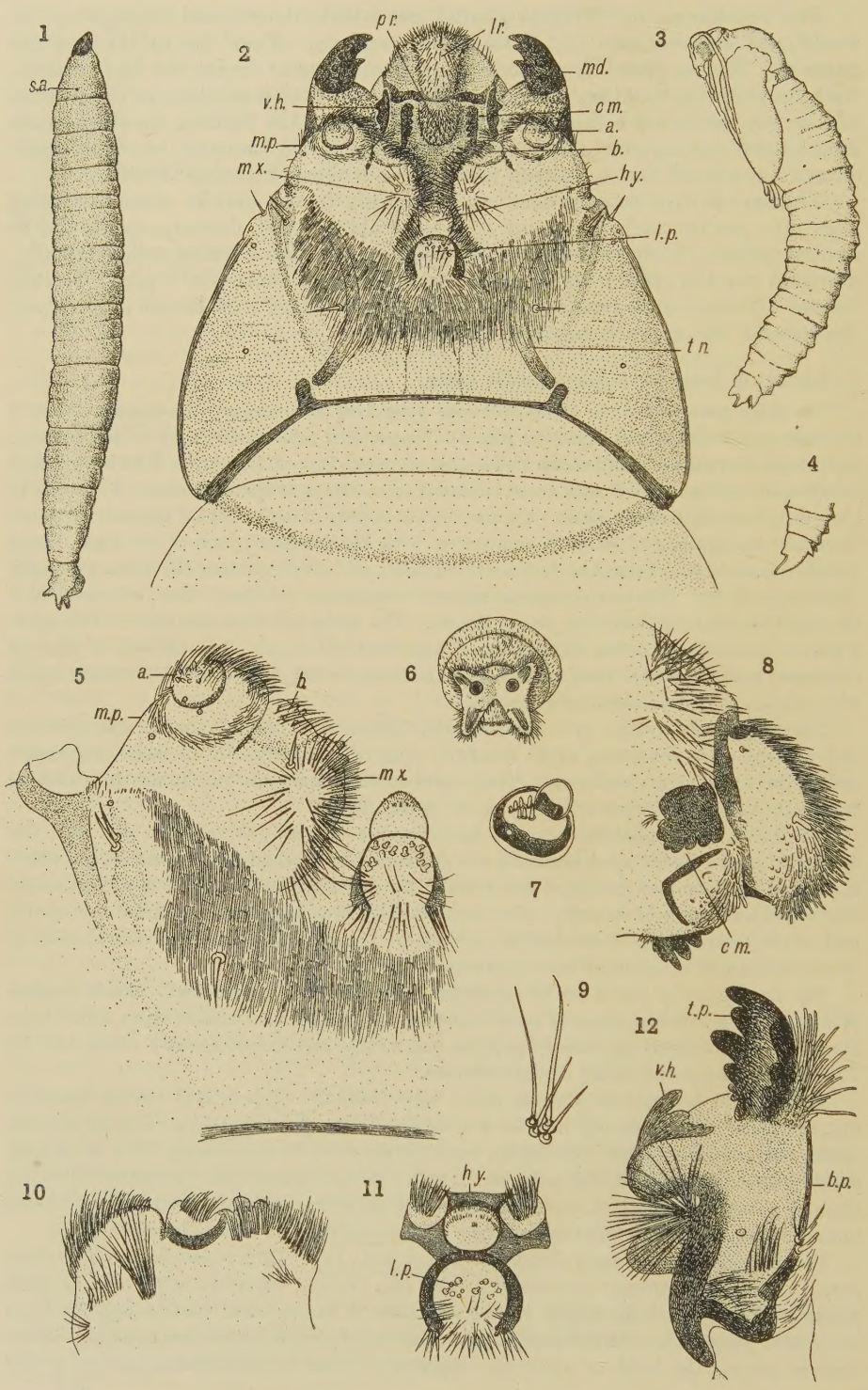
The respiratory system is amphipneustic. There is a pair of prothoracic spiracles (fig. 1, s.a.), each consisting of an eccentric plug of scar cuticle from which trabeculae radiate to an annular peritreme. The postabdominal spiracles are similar in structure except that they are larger and the plug is central (fig. 6).

The larva is eucephalous, *i.e.*, the head capsule is complete and free (fig. 2). The epicranial plates do not meet ventrally but are united by a broad area of thin cuticle which is covered by numerous groups of fine hairs. The posterior border of the head is strongly sclerotised and a pair of tentorial rods (tn.) extends forwards and upwards from the ventral part of the posterior border to near the antennae. On both the dorsal and ventral surfaces of the head there are sensory hairs and sensory pits.

The antennae are borne on the anterior lateral borders of the head. Each consists of a strongly sclerotised annular band enclosing an area of thin cuticle from which arise about six small cylindrical sensory papillae and a large bell-shaped sensory vesicle (fig. 7). The eyes are borne externally to the antennae.

The labrum projects as a stout fleshy lobe from the clypeus and curves ventrally (fig. 2, lr., fig. 8). Anteriorly it bears a number of sensory processes and a series of long, closely-set, cuticular hairs. Ventrally, near the entrance to the mouth, there is another fleshy prominence covered with hairs (fig. 2, pr.). At each side of this prominence there is a strongly sclerotised, toothed, comb-like, sclerite (figs. 2, 8, cm.) representing the structures termed by some authors (Feuerborn, 1933) " premandibles " in other dipterous larvae.

The mandibles are strongly developed (figs. 2, md., 12). Each is divided into two main parts. A terminal strongly sclerotised portion (fig. 12, t.p.) bears two series of large teeth orientated nearly at right angles to one another. A larger basal portion (fig. 12, b.p.) articulates posteriorly with the head capsule and on its medial border it is expanded into a dentate process the teeth of which are opposed to those of the anterior portion of the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mandible (figs. 2, 12, v.h.). At the point of junction between the basal and terminal parts, on the dorsal surface, there arises a fan of rigid hairs. On the basal piece there is a fan of hairs near the middle of the internal border, and, on the dorsal surface, there are two sensory pits, a few hairs, and two branched sensory setae on the external border.

The maxillae are oblong fleshy structures (figs. 2, 5). Each is divided into two regions : the maxilla proper (mx.); and the palp (m.p.) which forms a fleshy lobe lying external to the maxilla proper. The maxilla proper is more or less square and has two blunt processes dorsally on its anterior border, and on the medial border there are several long, stout, curved, setae projecting towards the middle line. On the ventral, or external, surface there are many fine hairs, a circle of long broad hairs, a stout sensory seta and a fringe of long hairs on the medial border (fig. 5). There are several groups of long hairs on the dorsal or internal surface (fig. 10). The maxillary palp has, on the distal part of the ventral surface, a group of sensory papillae surrounded by an annular band of cuticle, representing sensory organ " a " (figs. 2, 5, a.), outside of which there is a band of fine hairs. Internal to this, on the anterior border there is another group of sensory papillae surrounded by a weak cuticular band, within which there are many fine hairs, and this represents sensory organ " b " (figs. 2, 5, b.). There are two sensory pits on the ventral surface (fig. 5) and groups of long hairs on the dorsal surface (fig. 10).

The labium (= prementum of De Meijere, 1916) is formed of a semi-circular plate. The anterior region bears about 12 sensory papillae which are arranged in two groups and represent the fused labial palps. Posteriorly there are a number of long, broad setae (figs. 2, 11, l.p.). Dorsal to the labium, and separated from it by the opening of the salivary duct, lies the hypopharynx which bears two circular areas of thin cuticle, from each of which arises a tuft of long hairs, and a median circular area bearing rows of short setae (figs. 2, 11, hy.).

The internal anatomy has been described by Keilin (1912). The entrance of the oesophagus into the mid-gut is guarded by a simple valve and the mid-gut is large and simple and is devoid of gastric caeca. The hind-gut is divided into a swollen anterior part lined with flat epithelial cells bearing groups of recurved cuticular spines and a narrow posterior part which makes a dorsal loop before opening at the anus. There are four malpighian tubules which unite in pairs to open by two common ducts into the anterior part of the hind-gut. The salivary glands are small and have the form of simple elongated sacs which are folded upon themselves dorsally.

According to the description given by Karandikar (1931) the internal anatomy of *T. maculipennis* Meig. is similar to that of *T. hiemalis.*

2. Pupa of *Trichocera hiemalis.*

The pupa is free and has secondary folds obscuring the abdominal segmentation (fig. 3). There is a ring of recurved hooklets around the posterior margin of each abdominal segment. The respiratory system is peripneustic and consists of a pair of thoracic horns and six pairs of abdominal spiracles. The legs are superposed. The last abdominal segment differs in the two sexes. In the male (fig. 3) it is short and broad with stout lobes, whereas in the

FIGS. 1–12.—TRICHOCERIDAE. *T. hiemalis* De Geer : 1, fully grown larva, lateral view, showing free head capsule, presence of prothoracic spiracles and intercalary rings; 2, head, ventral view; 3, male pupa, lateral view; 4, posterior end of female pupa, lateral view; 5, right maxilla, external view, and labium, ventral view; 6, end view of post-abdominal segment showing spiracles and surrounding fleshy lobes; 7, antenna; 8, labrum, lateral view, showing comb-like sclerites, or " premandibles "; 9, setae representing the sensory vestiges of the thoracic legs; 10, maxilla, internal view; 11, labium and hypopharynx; 12, mandible, ventral view—this is probably an old specimen and the terminal teeth are blunt and uneven, but normally the teeth are regular and sharply pointed as in fig. 2.

female (fig. 4) it is narrower and the lateral lobes are longer than the other lobes in the female or than the corresponding lobes in the male.

The morphology of the early stages of *Trichocera regelationis* (L.) has been described by Rhynehart (1924) and of *T. maculipennis* by Karandikar (1931); and in both these species the early stages are very similar to those of *Trichocera hiemalis*.

III. Anisopodidae.

Edwards (1928) included in the family Anisopodidae the five genera *Anisopus* Meigen, 1804 (= *Rhyphus* Latreille, 1805); *Lobogaster* Philippi, 1865; *Olbiogaster* Osten-Sacken, 1886; *Mycetobia* Meigen, 1818; and *Mesochria* Enderlein, 1910.

The larvae of all these genera are found in moist situations where there is abundance of decomposing organic matter. The free pupae are found in the same medium as the larvae.

A. *Anisopus* Meigen.

1. Early stages of the genus *Anisopus*.

The earliest information about the larvae of *Anisopus* is due to Réaumur (1740), who stated that the larvae are common in September in cow dung. The short description which Réaumur gave of the larvae and pupae is just sufficient to show that he was dealing with *Anisopus* but it is much less precise than is characteristic for most of his observations.

Curtis (1826) cited Latreille as saying that the "larvae inhabit houses, and feed upon decaying and moist linen."

Guérin-Ménéville (1829–1844; date of plate 1835) also gave figures of the larva and pupa, but the figures are very inexact and the rose colour of the larva depicted is known to be a post-mortem change characteristic for the species. It is not possible to recognise the genus from these figures.

A decided advance was made by Dufour (1849), who described and figured both the larva and the pupa. Although both the descriptions and the figures are in places incorrect, the larva and pupa can be recognised easily from the figures.

Perris (1870) gave the most complete and exact description of this species. In addition to a description of the external morphology of the larva, the mouth-parts, antennae and eyes are also described with the correct terminology—mandible, maxilla, labrum and so on. Nevertheless the description and figures of the larval head are incomplete and lack precision. According to Perris the larvae live in decomposing vegetable matter such as rotting potatoes, lemons and melons.

Beling (1872) found larvae of *Anisopus punctatus* (Fabr.) in cow dung and larvae of *A. fenestralis* (Scop.) in decomposed potatoes in a cellar. He described the larvae and pupae but his descriptions are not accompanied by figures and can be understood only by those who have studied the larvae and pupae of these species.

In his bibliography of papers on the larva of *A. fenestralis*, Brauer (1883) gave the following reference: "E. Hartvinen, *Linn. Soc. Journ. Proc. Zool.* Vol. VI, 1862, p. 1–3, Holzschnitt, Mundteile und Kopf," but examination of this work, which is entitled "Description of a curious form of Dipterous Larvae," reveals that it deals with a Ceratopogonine larva and not with an *Anisopus* larva.

Osten-Sacken (1892) with regard to *Anisopus* merely mentioned that in the

larva of *A. punctatus*, from America, the prothoracic spiracles have three clefts and not two as was stated by Perris.

Finally one of us (D. K.), in a work on the larva of *Trichocera* (Keilin, 1912), has given a detailed figure of the head of a fully grown larva of *Anisopus fenestralis*.

As stated by the authors cited above, larvae of *Anisopus* may be found in all kinds of decomposing vegetable matter such as potatoes, beets, mouldy decaying cardboard reduced to a glutinous mass and also in the slime flux flowing from wounds in trees. Usually they occur in company with larvae of *Scatopse notata* L., *Lonchaea chorea* Fabr., Mycetophilids and Borborids. The larvae of *A. fenestralis* may be found throughout the year in such habitats; and in winter they have been found in half-frozen beetroots, the larvae being almost inactive and surrounded by crystals of ice.

Larvae of *Anisopus* move actively in a serpentine manner in the medium in which they live. If they are removed from the semi-fluid medium and are placed upon a solid surface it can be seen that they progress with the help of their mandibles, which alternately make rapid movements forwards and backwards and so act as locomotory appendages. In fluid media only the posterior rosette is visible floating on the surface, the rest of the body being immersed in the putrid mass. The larvae feed upon the decomposing substances in the medium.

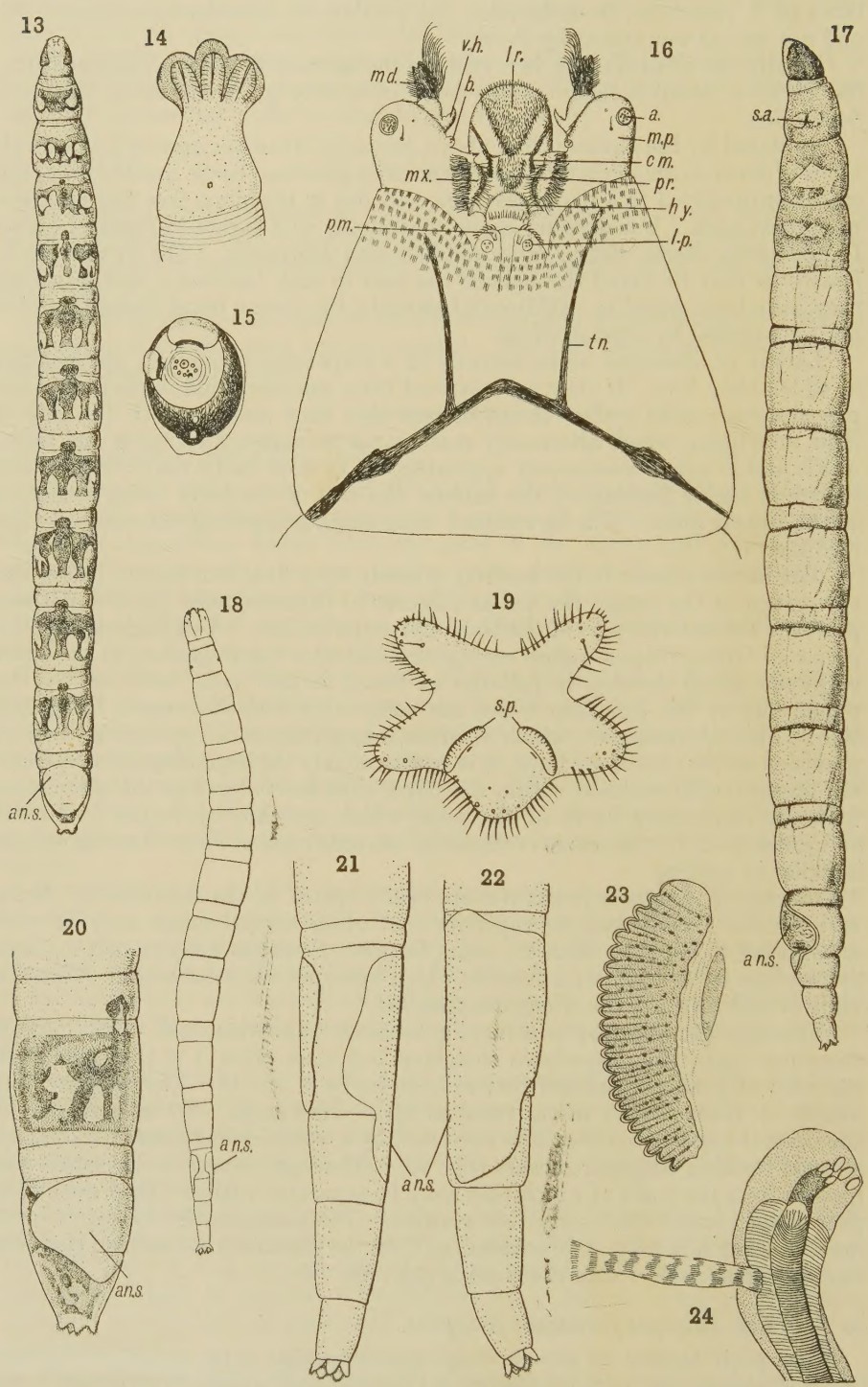
The larvae pupate in the medium wherein they live, but shortly before the emergence of the imago the pupae migrate to the less moist parts and there protrude the anterior part of the body above the surface. This migration of the pupae of Orthorrhapha before emergence, and also the migration to the open of pupae which develop in galleries in wood, is not really achieved by the pupae but by the imagines which are completely formed beneath the pupal skin. This phenomenon, which is often interpreted as a mysterious kind of prevision on the part of the pupa, is in reality merely the beginning of emergence : the imago is still enclosed within the pupal skin but it has lost the connection with the respiratory horns of the pupa which are thus no longer functional and, consequently, the imago is attracted towards regions where the atmosphere is richer in oxygen.

Larvae of *Anisopus fenestralis* are easily reared in the laboratory. Males and females readily pair in captivity and often several males may be seen attempting to copulate with the same female. Sometimes males may be seen attempting to copulate with females which have just emerged and of which the body is still soft and the wings unexpanded.

The eggs are enclosed in a large gelatinous mass when laid. The mass is sometimes spherical, sometimes elongated but most often it is U-shaped with particles of detritus enclosed between the limbs of the U. The eggs are just visible by transparency of the mass as little white spots. By compression of the mass it can be seen that it is traversed by a veritable network of refringent strands forming irregular meshes (fig. 40). The eggs appear to lie within the meshes from the walls of which they may be separated easily. They are small, pear-shaped and have a very thin chorion. The smallness of the egg is most marked when it is fully embryonated, as then the embryo is so confined that it is doubled upon itself within the chorion (fig. 39).

2. Larva of *Anisopus fenestralis* (Scopoli).

When newly hatched the larva is morphologically similar to the mature larva except that it is metapneustic, more transparent and that the head is larger in proportion to the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body at hatching than in old larvae. The latter fact, as has been noted in *Trichocera* (Keilin 1912), arises through the growth of the head being much slower than that of the rest of the body.

The fully grown larva of *A. fenestralis*, when ready to pupate, is 12–14 mm. long (fig. 17). The body is long and narrow and is formed of a small, free, well-sclerotised head, 3-thoracic and 8 abdominal segments. These segments correspond to true metameric somites but there is a number of secondary folds which form supplementary segments that increase the apparent number of segments to 20. Though the integument is yellow the underlying organs show through it and give the body a pink colour, and there are dark, violet-brown patches on each thoracic segment. The colour of the patches is due to inclusions in the parietal layers of the fat-body.

The respiratory system is amphipneustic. The prothoracic spiracles have three papillae each (figs. 14, 24). The postabdominal spiracles open between five fleshy lobes, bordered with long setae, which terminate the 8th abdominal segment (fig. 19, s.p.). Each spiracle is crescentic and has about 23 clefts (fig. 23).

On the ventral surface of each thoracic segment there are two groups of sensory hairs, each composed of 2 long and 2 short hairs, connected with the imaginal discs of the legs (fig. 34).

The 8th abdominal segment is divided into 5 secondary rings, and the anus opens ventrally between the 1st and 2nd of these rings. The anus is surrounded by a shield-like thickening lined by very large hypodermal cells (fig. 17, an.s.).

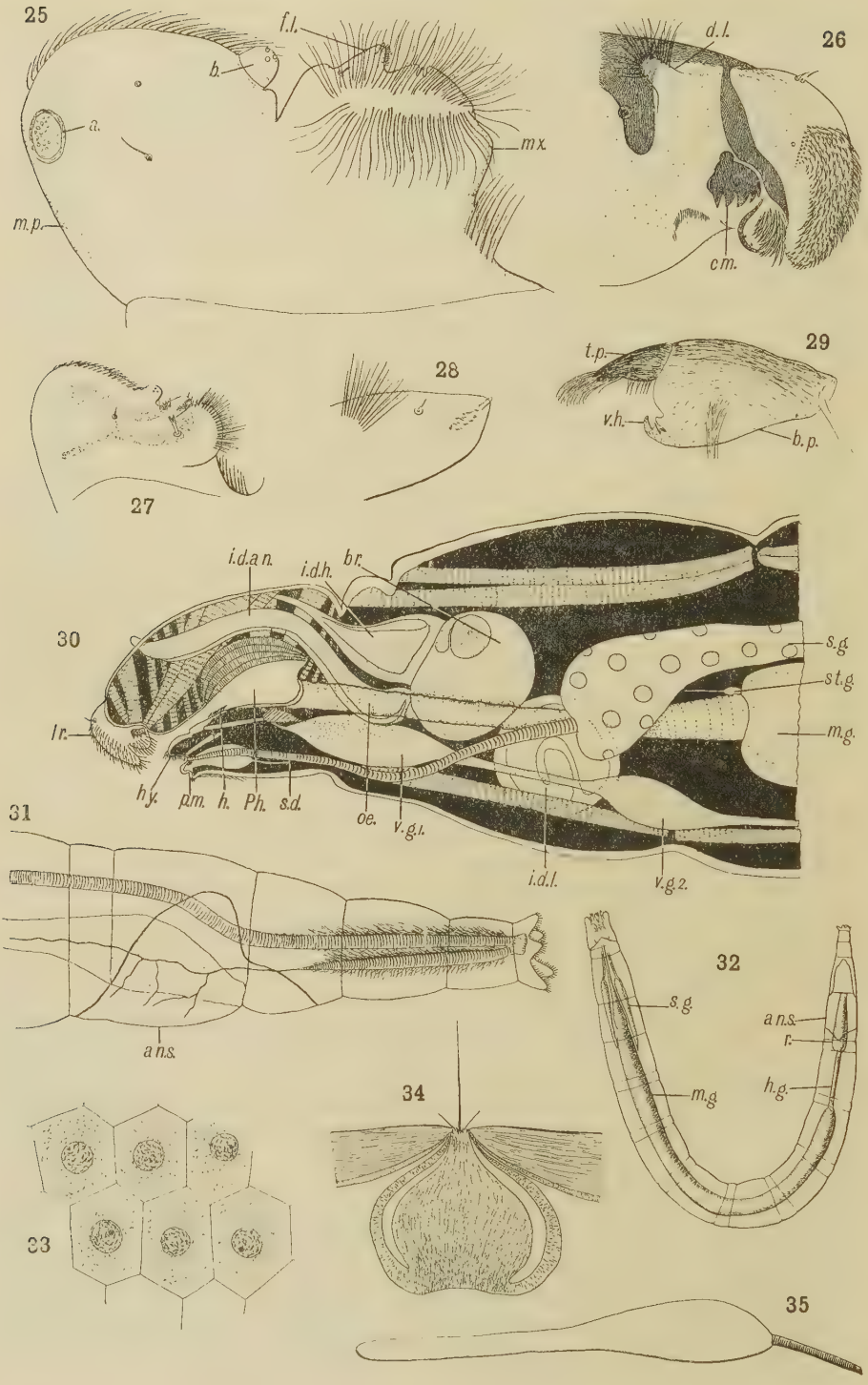
The head capsule (fig. 16), which is free and complete, is strongly sclerotised dorsally but only weakly so ventrally, where it shows about four rows of tufts of fine hairs. A pair of tentorial rods extends from near the antennae to the ventro-posterior margin of the head (tn.). The antennae are composed of an annular band of strong cuticle in which there are two sensory pits (figs. 15). The annular band is covered with a thin cuticular membrane upon which are borne a group of sensory papillae and two bell-shaped sensory vesicles. The presence of two bell-shaped sensory vesicles is a curious character which appears to be unique amongst dipterous larvae.

The labrum projects as a fleshy cushion with, dorsally, a pair of sensory hairs and some sensory pits, and, antero-ventrally, a shield-shaped area densely covered with small curved setae (figs. 16, lr., 26). A band of cuticle on each side embraces the labrum laterally and, attached to the ventral terminations of these bands, there is on each side a comb-like sclerite or " premandible " (figs. 16, 26, cm.). Between the " premandibles " there is a medio-ventral fleshy cushion covered with setae and sensory papillae (fig. 16, pr.). On each side of the labrum, in the dorso-posterior region, there is a fleshy lobe bearing a number of large setae (fig. 26, d.l.).

The mandibles (fig. 16, md., 29) are formed of two portions: a terminal strongly sclerotised piece ending in two teeth and bearing brush-like groups of long curved setae (fig. 29, t.p.); and a larger basal piece (fig. 29, b.p.) of which the internal border is expanded into a dentate process (figs. 16, 29, v.h.).

The maxillae (figs. 16, 25, 27) are soft fleshy organs and each is divided into two portions, an outer, the maxillary palp (m.p.), and an inner, the maxilla proper (mx.). The maxillary

FIGS. 13–24.—ANISOPODIDAE. Larvae: 13, *Anisopus punctatus* (Fabr.), fully grown larva, ventral view; 14, *A. fenestralis* (Scop.), anterior spiracle; 15, *A. cinctus* (Fabr.), antenna (the antenna of *A. fenestralis* is similar); 16, *A. fenestralis*, head, ventral view; 17, *A. fenestralis*, fully grown larva, lateral view; 18, *A. picturatus* Knab, fully grown larva, dorsal view; 19, *A. fenestralis*, end view of 8th abdominal segment; 20, *A. punctatus*, lateral view of 8th abdominal segment; 21, *A. picturatus*, dorso-lateral view of 8th abdominal segment; 22, *A. picturatus*, ventro-lateral view of 8th abdominal segment; 23, *A. fenestralis*, postabdominal spiracle; 24, *A. fenestralis*, anterior spiracle undergoing moult.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palp bears two circular areas (" a " and " b ") within which there are groups of sensory papillae; and also one sensory pit, one sensory seta and a fringe of numerous hairs. The inner portion, or maxilla proper, bears several sensory processes and near the internal border there are numerous long hairs. On the anterior margin there is a triangular fleshy lobe (figs. 25, f.l., 28) which bears, terminally, a sensory process, and, internally, a sensory seta, a group of long hairs and tufts of small hairs. On the internal face of the maxilla proper there is a single branched seta and a semi-circle of long hairs near the medial border (fig. 27).

The labium, or prementum according to the nomenclature of De Meijere (1916), is fringed with setae and bears two circular areas, each with several sensory papillae, which represent the labial palps (fig. 16, l.p.). The opening of the salivary duct separates the labium from the hypopharynx which consists of a rounded lobe bearing a fringe of fine hairs and a transverse row of long setae (figs. 16, 30, hy.).

The internal anatomy. The oral cavity expands into a deep pharynx (fig. 30, Ph.) the entrance to which is guarded by a mat of backwardly directed hairs arising from the ventral wall (fig. 30, h.). The salivary glands are simple and sac-like (figs. 30, s.g., 35) and the common salivary duct (fig. 30, s.d.) opens between the prementum and the hypopharynx. The pharynx is deep dorso-ventrally and the dorso-posterior region is produced backwards so that the opening to the oesophagus is more or less ventral. The oesophagus (fig. 30, oe.) is a simple straight tube which extends to the posterior border of the 1st thoracic segment and there opens into the mid-gut. The mid-gut (fig. 32, m.g.) is devoid of caeca and extends as a simple tube as far as the 7th abdominal segment, where it leads into the narrow posterior intestine (h.g.) that extends as far as the 8th abdominal segment and there opens into the wide rectum (r.). The anus opens ventrally about the middle of the 8th segment.

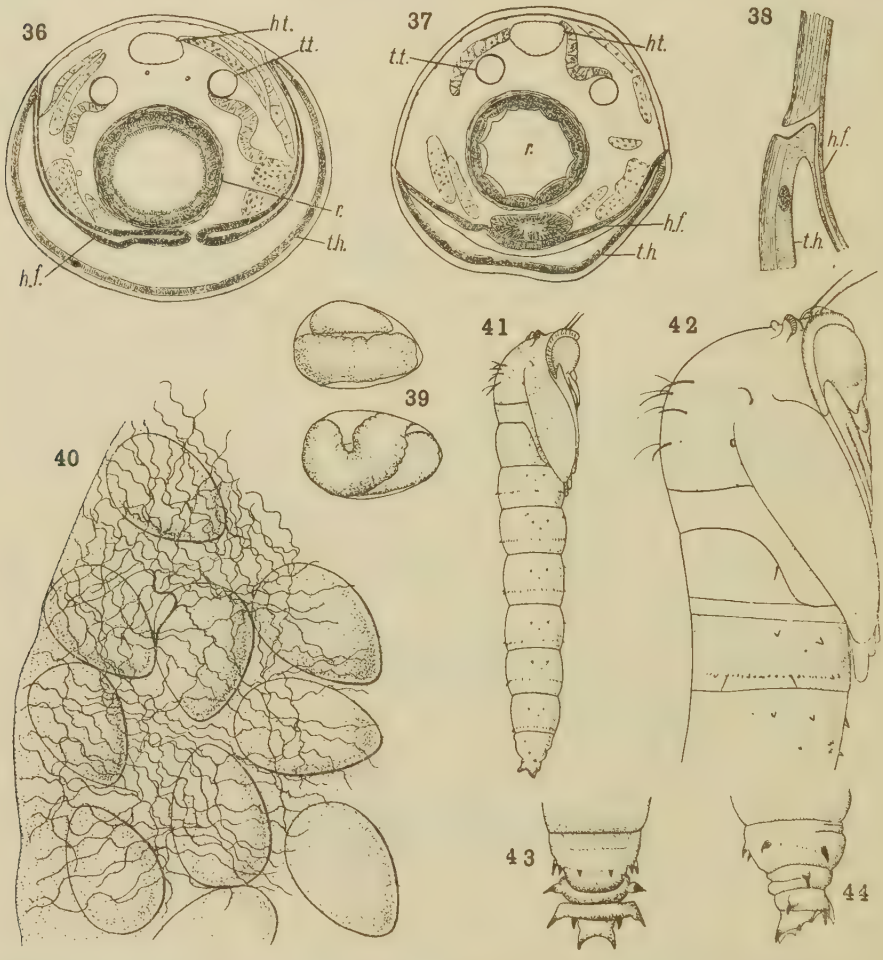
The shield-shaped area on the 8th abdominal segment (figs. 17, 31, 32, an.s.) is formed of large hexagonal hypodermal cells with densely granular contents (fig. 33). The line demarcating this area is seen, in transverse sections, to be formed of a distinct break in the cuticle of the body-wall (fig. 38). Beneath this break the hypodermis is infolded (figs. 36, 37, 38, h.f.) so that folds formed of two layers of hypodermal cells extend into the body of the larva and embrace the gut and other internal organs. In places the edges of the folds from each side approach each other closely (fig. 36, h.f.) and in the anterior and posterior regions they form a diaphragm separating the gut and other organs from a ventral chamber (fig. 37, h.f.). The large hypodermal cells of this area are richly supplied with tracheae derived from ventral tracheal trunks which arise from the postabdominal spiracles and run parallel with the main tracheal trunks on each side to the middle of the 8th segment. They there send off a number of branches to the shield-shaped area before continuing as the ventro-lateral tracheal trunks (fig. 31). The function or significance of this peculiar

FIGS. 25–35.—ANISOPODIDAE. *Anisopus fenestralis* (Scop.). Larva: 25, right maxilla, external view; 26, labrum, lateral view; 27, left maxilla, internal view; 28, internal view of sensory lobe of maxilla; 29, mandible, lateral view; 30, optical section through head and 1st thoracic segment (this figure was drawn from a preparation made in the following manner. The anterior part of a larva was fixed, stained *in toto* with borax carmine and embedded in paraffin wax. Longitudinal sections were cut from one side until approximately the middle line was reached. Then the block was reversed and sufficient longitudinal sections were cut off the opposite side to give a flat surface. The remains of the larva were then dissolved out of the paraffin wax and mounted in canada balsam); 31, lateral view of 8th abdominal segment showing tracheal trunks; 32, fully grown larva of *A. picturatus* Knab, ventral view showing alimentary canal and salivary glands (the internal anatomy of *A. fenestralis* is similar); 33, surface view of large hypodermal cells which form the anal shield; 34, section of imaginal disc of leg, showing its connection with the group of sensory hairs; 35, salivary gland.

arrangement of large hypodermal cells and the infolding of the hypodermis is unknown but it is possible that the enlarged hypodermal cells may contain symbionts.

3. Larvae of some other species of *Anisopus*.

Larvae of the species *Anisopus picturatus* Knab and *A. punctatus* (Fabricius) have also been examined in the course of this work. While the two species are



FIGS. 36–44.—ANISOPODIDAE. *Anisopus fenestralis* (Scop.): 36, transverse section of larva passing through middle of the anal shield, showing layer of thickened hypodermal cells and the inflected folds of hypoderm; 37, a similar section farther back; 38, section showing the break in the chitin of the body-wall at the margin of the anal shield; 39, eggs with embryos doubled up inside; 40, part of an egg mass; 41, pupa, lateral view; 42, anterior part of pupa, lateral view; 43, posterior end of pupa, ventral view; 44, posterior end of pupa, lateral view.

very similar in general morphology to *A. fenestralis* they differ from it and from each other in some respects. *A. punctatus* (fig. 13) differs from *A. fenestralis* in having the characteristic dark markings extending over all the segments of the body, in having the last abdominal segment divided into only two rings,

and in the perianal shield being small and having the anal opening near its posterior margin (fig. 20, an.s.). The perispiracular fleshy lobes surrounding the postabdominal spiracles are much shorter in *A. punctatus* than in *A. fenestralis*. *A. picturatus* differs from the other two species in having the perianal shield more elongated and extending farther towards the dorsal surface of the segment involved (figs. 18, 21, 22, 32, an.s.).

4. Pupa of *Anisopus fenestralis*.

The pupa is about 8·5 mm. long and has the legs superposed (fig. 41). There is a pair of sessile prothoracic respiratory horns, and in addition there is one pair of thoracic and six pairs of abdominal spiracles. There is a pair of long, frontal hairs and the thorax bears four pairs of short hairs (fig. 42). Each abdominal segment, except the last, has near the anterior border 3 pairs of hooks, one ventral and two lateral; and, near the posterior border, a ring of small hooklets of which some, spaced at irregular intervals, bear long sensory setae (figs. 41, 42). The posterior abdominal segment has 7 pairs of strongly sclerotised hooks (figs. 43, 44), and two pairs of much smaller hooks on the posterior margin which are visible only from the lateral aspect (fig. 44).

B. *Mycetobia* Meigen.

1. Early stages of *Mycetobia*.

The earliest description of *Mycetobia* is that by Lyonet (1832), who described and figured the larva, pupa and adult. He noted that the larva moved by means of the " barbillions " (mandibles) of the head and that the three thoracic segments showed pretty brown patterns. The larvae live in moist places, or even in water, and the pupae are armed with two rows of small backwardly directed spines. The pupal stage lasts four days. Guérin-Méneville (1829–1844) gave inexact figures of the pupa and of the adult of *Mycetobia thoracica* Guérin. Westwood (1840) briefly described the larva and pupa of *Mycetobia pallipes* Meigen; and Walker (1856) mentioned that *M. pallipes* is rare and inhabits the decayed trunks of trees. Dufour (1849) made a more detailed study of the larva and pupa of *M. pallipes* and pointed out the close resemblance between the larva and that of *Rhyphus fenestralis*. Perris (1870) gave the most complete and exact account available of the early stages of *M. pallipes* and emphasised the relation between *Rhyphus* and *Mycetobia*; especially as regards the respiratory system, which is amphipneustic in these larvae in contrast to the peripneustic larvae of MYCETOPHILIDAE. Weijenbergh (1874) gave some information on the biology of *M. pallipes*.

Osten-Sacken (1892) again discussed the question of the relationship of the larvae of *Rhyphus* and *Mycetobia* and, after citing the work of Lyonet, Dufour, Perris and others, he concluded : " If there is a real relationship between the larvae of *Mycetobia* and *Rhyphus* we have a right to expect a corresponding relationship among the imagoes. But as this relationship does not exist there is a problem yet to solve."

Johannsen (1909) gave a short description, without figures, of the larva and pupa of *Mycetobia divergens* Walker and placed the genus *Mycetobia* in the subfamily MYCETOBIINAE of the MYCETOPHILIDAE together with the genera *Palaeoplatyura*, *Ditomyia* and *Symmerus*. Malloch (1915) described the larva and pupa of *M. divergens* and concluded that *Mycetobia* diverges from the family MYCETOPHILIDAE only in the absence of abdominal spiracles and that the genus should remain in that family.

Later, the work of Edwards (1916) and Keilin (1919) finally determined the

transference of the genus *Mycetobia* from the MYCETOPHILIDAE to the ANISOPODIDAE (Edwards, 1928).

2. Larva of *Mycetobia pallipes* Meig.

The eggs of *M. pallipes* are pear-shaped and are laid embedded in a gelatinous mass which is attached to the substratum (fig. 67).

The larvae are to be found in moist rotten wood and also in the slime-flux running from wounds in trees.

The mature larva is about 10 mm. long and in general appearance it resembles that of *Anisopus fenestralis* (fig. 47). The larva is composed of a head, three thoracic segments and 8 abdominal segments. The 1st thoracic and the 8 abdominal segments have each an intercalary ring occupying the anterior quarter of the segment. The 8th abdominal segment, in addition to the anterior ring, is again subdivided so that it appears to be formed of three segments (fig. 45). There is a large perianal shield, formed of thickened hypodermal cells, which occupies all the ventral, lateral, and part of the dorsal surface of the anal segment posterior to the intercalary ring (fig. 45, an.s.). The groups of sensory hairs connected with the imaginal discs of the legs on the thoracic segments are composed of 4 hairs each, two long and two short (fig. 57).

The respiratory system is amphipneustic. Each prothoracic spiracle is composed of 19 papillae and a large felt chamber (f.c.) with well-defined internal (i.s.) and external (e.s.) scars (fig. 49). The postabdominal spiracles are terminal and are surrounded by 5 obscure lobes fringed with long setae. The spiracles are oval and contain about 12 clefts (fig. 50, s.p.).

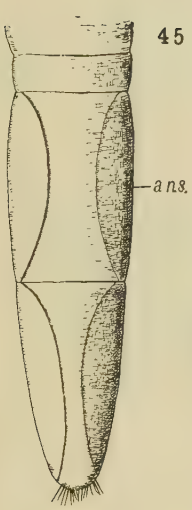
The head capsule, which closely resembles that of *Anisopus fenestralis*, is free, complete and strongly sclerotised above (fig. 46). The antennae (fig. 51) consist of a deep, strongly sclerotised basal portion which bears an asymmetrical bell-shaped sensory vesicle and an elevated group of sensory papillae.

The labrum (figs. 46, lr., 52) projects as a fleshy lobe bearing a pair of long sensory hairs dorsally, 2 pairs of sensory pits laterally, and continuing ventrally as a fleshy cushion densely covered with short setae. There is a pair of lateral sclerotised bands and, between the ends of these, there is a medio-ventral fleshy pad covered with small curved setae (fig. 46, pr.). On each side of this pad there is a comb-like sclerite or " premandible " (figs. 46, 52, cm.).

The mandibles (fig. 54) consist of two parts : a strongly sclerotised terminal piece (t.p.) ending in three stout teeth and having a fan of long, rigid, curved hairs arising from the dorsal surface and a row of flat setae along the medial border; and a basal piece (b.p.) which is expanded on its medial border to form a dentate process (v.h.).

The maxillae (figs. 46, 53) are broad fleshy organs and each consists of two regions : an outer lobe, the maxillary palp (m.p.) bearing two circular areas (" a " and " b ") enclosing groups of sensory papillae (figs. 46, 53, a., b.), a marginal fringe of long hairs, and, on the ventral surface, three long sensory hairs; and an inner lobe, the maxilla proper (mx.). The maxilla proper has a dense ring of long setae and, on the anterior margin, a sensory papilla and a soft, narrow lobe bearing a terminal digitiform sensory process, a small sensory hair and several rows of short setae (figs. 53, 55, f.l., 56).

FIGS. 45–57.—ANISOPODIDAE. *Mycetobia pallipes* Meig. Larva : 45, 8th abdominal segment, dorsal view; 46, head, ventral view; 47, fully grown larva, dorsal view; 48, fully grown larva, showing alimentary canal and salivary glands; 49, anterior spiracle; 50, end view of 8th abdominal segment; 51, antenna; 52, labrum, lateral view; 53, right maxilla, external view; 54, mandible, external view; 55, left maxilla, internal view; 56, sensory lobe of maxilla; 57, setae, representing the sensory vestiges of the thoracic legs.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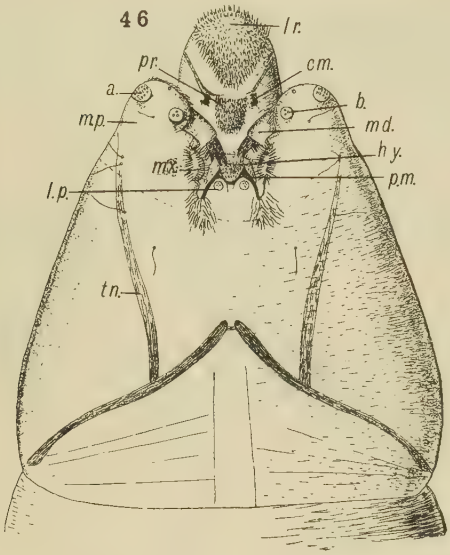
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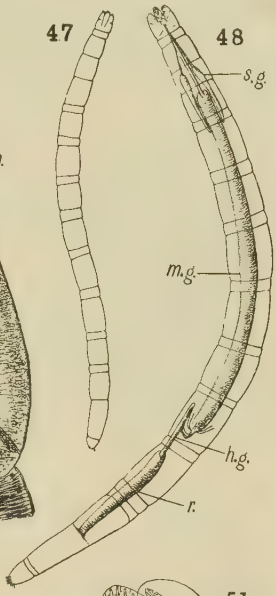
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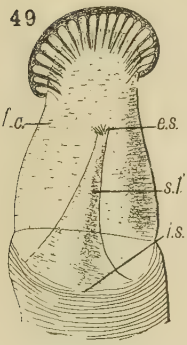
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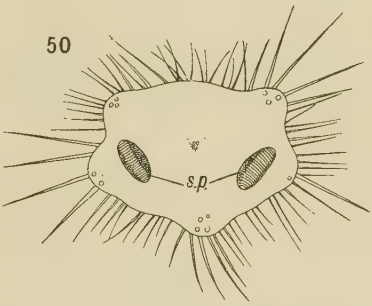
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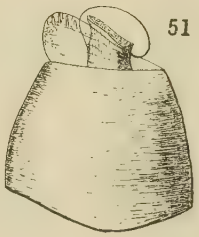
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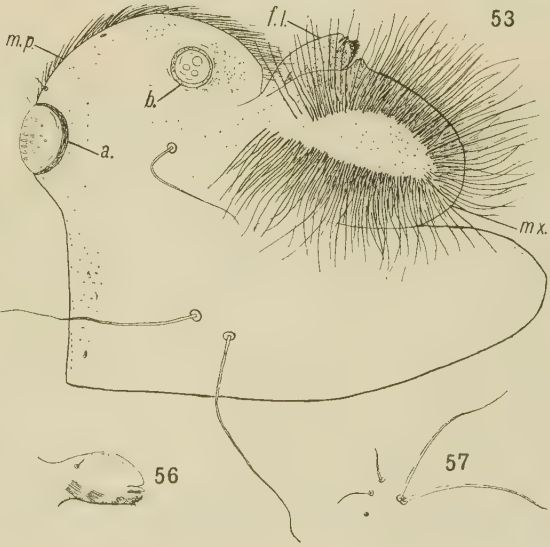
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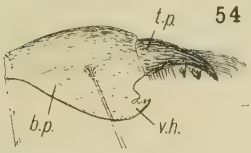
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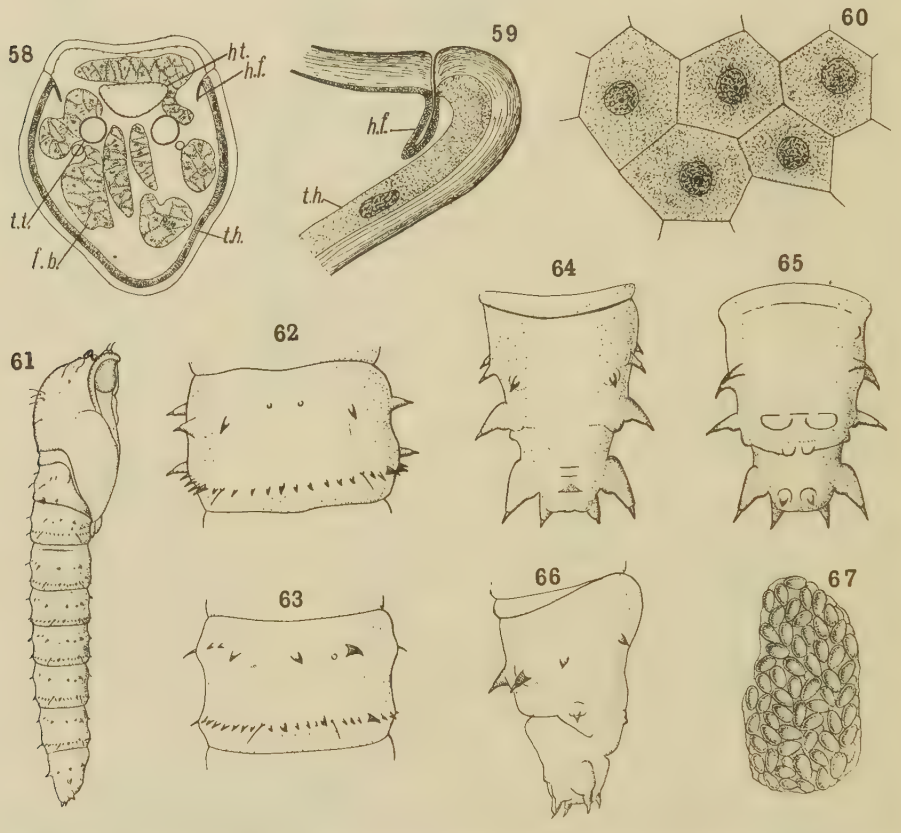
The labium, or prementum, consists of two heavily sclerotised pointed processes (fig. 46, p.m.), posterior to which there is a pair of annular bands enclosing groups of sensory papillae that represent the labial palps (fig. 46, l.p.). Dorsal to the prementum, and separated from it by the opening of the salivary duct, there is a fleshy hypopharynx (fig. 46, hy.).



Figs. 58–67.—Anisopodidae. *Mycetobia pallipes* Meig.: 58, transverse section of larva in region of perianal shield; 59, transverse section through body-wall of larva showing infolding of hypoderm at margin of perianal shield; 60, surface view of the large hypodermal cells which form the perianal shield; 61, pupa, lateral view; 62, dorsal view of abdominal segment of pupa showing the arrangement of the hooklets and spines; 63, lateral view of abdominal segment of pupa showing the arrangement of the hooklets and spines; 64, dorsal view of terminal segment of pupa; 65, ventral view of terminal segment of pupa; 66, lateral view of terminal segment of pupa; 67, egg mass.

The ventral surface of the head bears about 4 pairs of long sensory hairs and, near the postero-lateral limits of the labium, there are tufts of long soft hairs. Internally there is a pair of tentorial rods extending from near the bases of the antennae to the ventro-posterior margin (fig. 46, tn.).

The internal anatomy is very similar to that of *Anisopus fenestralis*. The salivary glands are simple and short (fig. 48, s.g.). The narrow straight oesophagus leads into the mid-gut (fig. 48, m.g.), which is devoid of caeca, and the mid-gut runs straight back to the hind-gut. Four malpighian tubules arise from near the junction of the mid-gut and the hind-gut.

The hind-gut is straight and narrow, but, unlike that of *Anisopus fenestralis*, it first turns forwards and makes a loop in the 6th abdominal segment before running back to expand into the wide rectum in the 7th abdominal segment (fig. 48, h.g.). The rectum (fig. 48, r.) ends in the anus, which opens ventrally about half-way towards the posterior end of the 8th abdominal segment. The anal shield (fig. 45, an.s.) is formed of a layer of large thickened hypodermal cells (figs. 58, 59, t.h., 60). It is limited by a complete break in the cuticle of the body-wall all round the margin, and at this break the hypoderm is reflected inwards to form a fold lined with thin cuticle (figs. 58, 59, h.f.). In *Mycetobia pallipes*, however, this fold is narrow and does not extend inwards to enfold the internal organs as in *Anisopus fenestralis*.

3. Pupa of *Mycetobia pallipes*.

The pupa of *M. pallipes* is about 6 mm. long and is very similar to that of *Anisopus*, except that the frontal hairs are shorter and that there are more numerous hooklets in the anterior ring around each abdominal segment (fig. 61). As in *Anisopus*, the hooklets of the posterior ring on the abdominal segments are backwardly directed and some of them terminate in long sensory hairs (figs. 62, 63). The last abdominal segment has eight pairs of hooks (figs. 64, 65, 66). The legs are superposed.

C. *Olbiogaster* Osten-Sacken.

Very little is known about the habits of either the adults or larvae of *Olbiogaster*. According to Edwards (1928) the larvae of *O. africanus* Edwards have been found in rot-holes in trees; and *O. scalaris* (Wiedemann) and *O. trinidadensis* Edwards have been obtained from rotten wood.

1. Larva of *Olbiogaster africanus* Edwards.

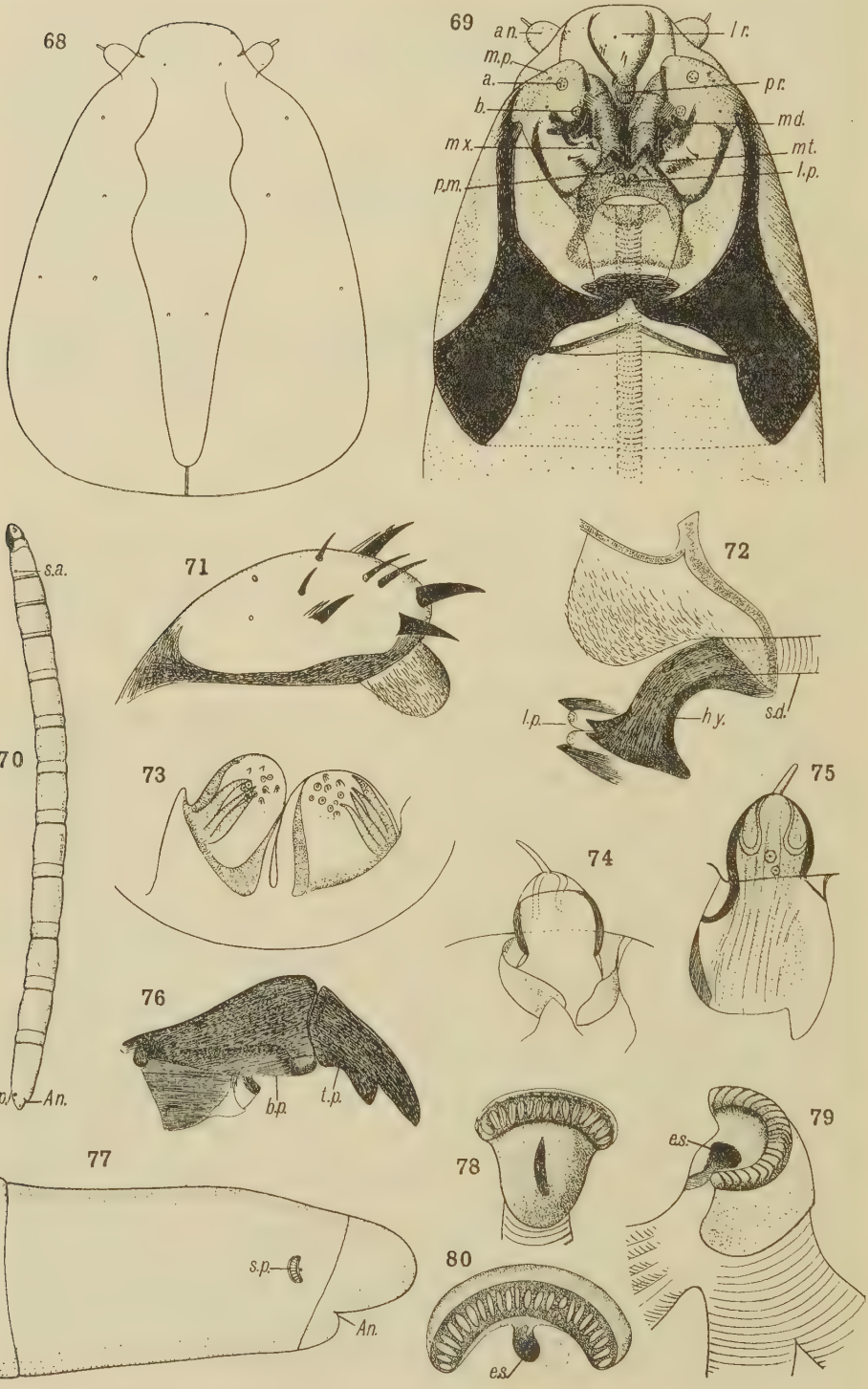
The mature larva is about 15 mm. long and is composed of a free head-capsule, 3 thoracic and 8 abdominal segments (fig. 70). There are intercalary rings separating all the segments. The body terminates in a short conical process and the anus is ventral and sub-terminal (fig. 70, An.). The respiratory system is amphipneustic. The prothoracic spiracles consist of about 16 papillae arranged fan-wise and have stout felt chambers and well-marked external scars (fig. 78). The postabdominal spiracles are placed laterally on the last segment and lie slightly anterior to the level of the anus (figs. 70, 77, s.p.). They project above the surface of the body, are crescentic in shape and have about 25 clefts, some of which may be subdivided into two or three smaller clefts (figs. 77, 79, 80). There is a dense black external scar near the middle of the concave side of the spiracular tubercle (figs. 79, 80, e.s.).

The head capsule (figs. 68, 69) is more strongly sclerotised than in *Anisopus* and dorsally it bears 7 pairs of sensory pits. The antennae are large and are inserted in a groove (fig. 69, an.). Each antenna consists of a strongly sclerotised dome-like basal segment bearing two sensory pits, and terminating in a finger-like sensory process (figs. 74, 75).

The labrum is fleshy with a pair of lateral sclerotised bands (figs. 69, lr., 71). It bears 2 pairs of sensory pits and a small number of large curved spines. There is a median ventral pad covered with setae between the ends of the sclerotised bands (fig. 69, pr.), but there are no comb-like sclerites (" premandibles ").

The mandibles (figs. 69, md., 76) are divided into two parts, both of which are strongly sclerotised. The terminal piece (t.p.) ends in strong teeth, but the basal piece (b.p.) is devoid of the dentate process present in larvae of *Anisopus*, *Mycetobia* and *Trichocera*, and there are no groups of long setae such as are present in these genera.

Each maxilla is formed of two lobes : an external lobe, the maxillary palp (fig. 69, m.p.), which bears two groups of sensory papillae (" a " and " b ") and a marginal tuft of setae;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and an inner lobe, the maxilla proper (fig. 69, mx.), which has some ventral and marginal sensory processes and bears a band of setae. There is a dark band of cuticle strengthening the anterior margin of the maxillary palps and extending for some distance along the anterior margin of the maxilla proper.

The labium is partly covered by a bidentate mentum (fig. 69, mt.), through which a bidentate prementum (p.m.) bearing the labial palps (l.p.) can be seen by transparency. The labial palps are conical fleshy processes bearing a group of about 10 sensory papillae terminally. From the base of each palp arises a group of four flattened setae (figs. 69, l.p., 73). The hypopharynx extends dorso-posteriorly from the labium in the form of a pair of heavily sclerotised, flattened, curved plates which are expanded ventrally and between the dorsal ends of which the salivary duct opens (fig. 72, hy.).

The ventral surface of the head is devoid of setae. The lateral regions of the posterior half are heavily sclerotised and, on each side, a narrow strip of dark cuticle extends forwards from the heavily sclerotised areas to near the bases of the maxillae. The lateral sclerotised areas give off ventro-median processes which are united in the mid-ventral line by a hexagonal area of dark cuticle (fig. 69).

2. Pupa of *Olbiogaster africanus.*

The pupa (fig. 81) is about 7 mm. long and differs greatly from those of the other genera dealt with in this paper. There are no frontal hairs and the prothoracic respiratory horns are very small. The thorax and the first abdominal segment are without spines. The 2nd abdominal segment has one stout spine on each side and the next 5 abdominal segments have a pair of stout spines on each side (figs. 81, 83). The last abdominal segment bears on its posterior margin 3 pairs of long stout spines the surface of which is finely spinulose (fig. 82).

D. *Mesochria* Enderlein.

The only material available for the study of the early stages of this genus was a single pupal skin of *Mesochria medicorum* Edwards, 1928, which was obtained from rotting banana fibre by Ingram and Macfie on the Gold Coast, Africa, in 1920 (Edwards, 1928).

1. Pupa of *Mesochria medicorum* Edwards.

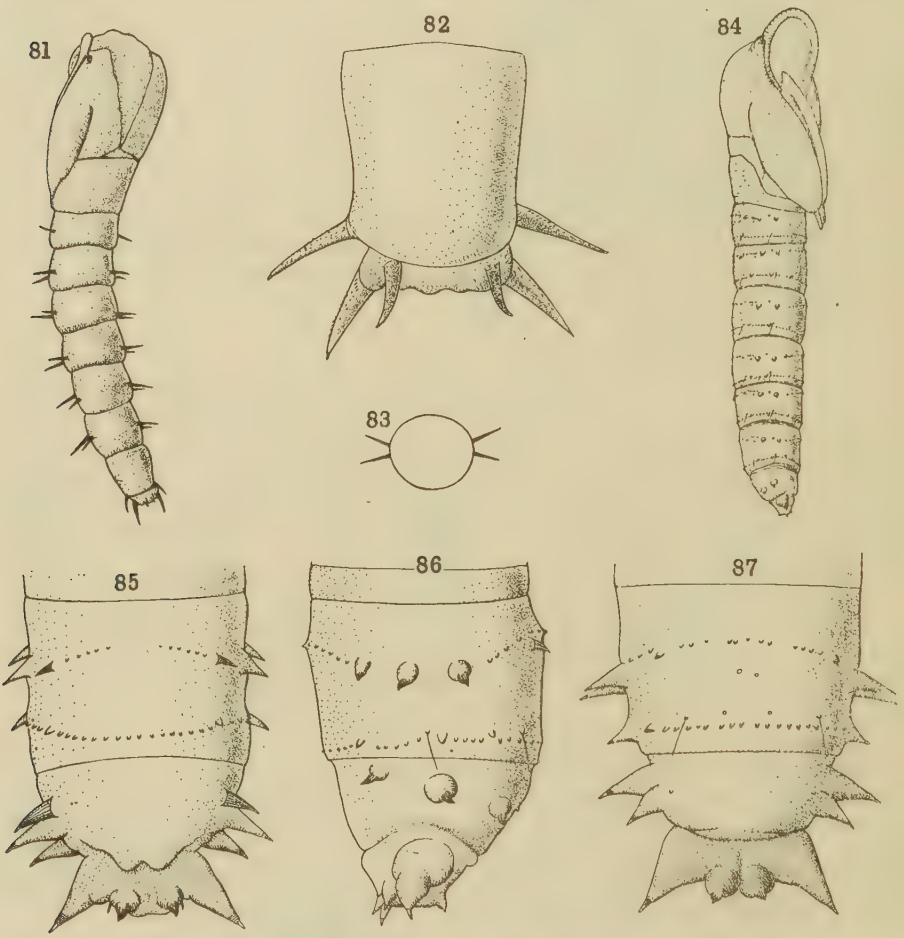
The pupa has short prothoracic horns (fig. 84). The legs are superposed and there are no frontal hairs. There is one pair of thoracic and six pairs of abdominal spiracles. The abdominal segments, except the 8th, have both anterior and posterior rings of hooklets and in both rings there are larger hooklets intermixed with the small ones (figs. 84–87). The 8th abdominal segment bears 5 pairs of stout hooks (figs. 85, 86, 87).

IV. Discussion.

The larvae of all the genera considered, *Trichocera*, *Anisopus*, *Mycetobia* and *Olbiogaster*, have a number of characters in common. They all have free and complete head capsules and bodies composed of 3 thoracic and 8 abdominal segments, although the number of true segments is obscured by the presence of intercalary rings or secondary folds. All these larvae are amphipneustic

FIGS. 68–80.—ANISOPODIDAE. *Olbiogaster africanus* Edwards. Larva: 68, head, dorsal view; 69, head, ventral view; 70, whole larva, lateral view; 71, labrum, lateral view; 72, labium and hypopharynx, lateral view; 73, labial palps; 74, antenna, ventral view; 75, antenna, dorsal view; 76, mandible, external view; 77, 8th abdominal segment, lateral view; 78, anterior spiracle; 79, postabdominal spiracle; 80, postabdominal spiracle, surface view.

and have only two pairs of functional spiracles, prothoracic and postabdominal. In the structure of the mouth-parts common features are present in the mandibles, formed of a basal piece and a terminal toothed piece; and in the maxillae, which are soft and fleshy and consist of two lobes, an outer, the maxillary palp,



Figs. 81–87.—Anisopodidae. *Olbiogaster africanus* Edwards and *Mesochria medicorum* Edwards. Pupae: 81, *Olbiogaster africanus*, dorso-lateral view of pupa; 82, *O. africanus*, terminal segment; 83, transverse section of abdominal segment of pupa of *O. africanus*, showing the arrangement of the lateral spines; 84, *Mesochria medicorum*, lateral view of pupa; 85, *M. medicorum*, ventral view of terminal segment of pupa; 86, *M. medicorum*, lateral view of terminal segment of pupa; 87, *M. medicorum*, dorsal view of terminal segment of pupa.

bearing two groups of sensory organs ("a" and "b"), and an inner, the maxilla proper, bearing sensory papillae and long setae.

More detailed examination, however, shows that the resemblance is not equally close between the larvae of the different genera. Larvae of *Trichocera*, *Anisopus* and *Mycetobia* have many structural characters in common. The head capsules of the larvae of these three genera all have tentorial rods and

more or less numerous groups of long hairs on the ventral surface. The antennae are composed of a basal segment surmounted by a number of sensory papillae and one, or two, characteristic bell-shaped sensory vesicles. In each of these genera the labrum has two ventral pads covered with setae and a pair of comb-like sclerites or " premandibles." The mandibles are composed of basal and terminal pieces of which the basal piece has the medial border produced into a dentate sclerite. At the junction of the two parts there are fan-like groups of long, rigid hairs. The labium is provided with groups of sensory papillae, representing labial palps, visible externally. The postabdominal spiracles are terminal and are surrounded by fleshy lobes fringed with setae. The sensory vestiges of the legs consist of groups of 4 setae, each group being formed of two long and two short setae. In all these genera the anus is ventral.

As regards the internal anatomy, larvae of *Trichocera*, *Anisopus* and *Mycetobia* agree in the following characters : There is a simple oesophageal valve guarding the entrance of the oesophagus into the mid-gut and the mid-gut is devoid of gastric caeca. The hind-gut is short and is either straight or forms a simple dorsal loop before opening at the ventral anus. There are four malpighian tubules which open in pairs into the anterior part of the hind-gut. The salivary glands are simple and sac-like and are either straight or are folded upon themselves.

The genera *Anisopus* and *Mycetobia* show additional points in common in the presence of a perianal shield of thickened hypodermal cells, and in having the embryos curved within the pear-shaped eggs which are laid embedded in gelatinous masses. In these features *Anisopus* and *Mycetobia* differ from *Trichocera*.

Larvae of *Olbiogaster*, while sharing the general features common to the four genera, differ markedly in detail from larvae of *Trichocera*, *Mycetobia* and *Anisopus*. In *Olbiogaster* the structure of the antennae is quite different as they consist of a basal segment bearing a terminal, digitiform process and the bell-shaped sensory vesicle, so characteristic of the other genera, is absent. The labrum of *Olbiogaster* larvae is very different from the labrum of larvae of *Trichocera*, *Mycetobia* and *Anisopus*, and is devoid of the comb-like sclerites. The mandibles of larvae of *Olbiogaster* differ from those of the other genera in the absence of fan-like groups of setae and of the dentate process on the medial border of the basal piece. The maxillae resemble those of the other genera except that they are more heavily sclerotised. In contrast to the other genera, larvae of *Olbiogaster* have a strong bidentate mentum which underlies the prementum. The ventral surface of the head capsule has areas of dense sclerotisation and does not bear groups of long hairs. The anus is sub-terminal in larvae of *Olbiogaster*, whereas it is ventral in larvae of *Trichocera*, *Anisopus* and *Mycetobia*; and the postabdominal spiracles of *Olbiogaster* larvae are not terminal but are placed laterally and lie anterior to the level of the anus.

The pupae of the genera *Trichocera*, *Anisopus*, *Mycetobia* and *Mesochria* are all very similar and agree in being strongly sclerotised, having the legs superposed, being hemipneustic, and in having rows of small hooklets on the first 7 abdominal segments and a series of strong hooks on the posterior segment. The pupa of *Olbiogaster* differs greatly from the pupae of the other genera because it is devoid of hairs or small hooklets, but has one or two pairs of large stout lateral spines on the first seven abdominal segments and three pairs of large spines on the 8th abdominal segment.

If larvae of these genera be compared with those of other Nematocera

it is seen that in general structure they show many differences from Mycetophilid larvae, most of which are peripneustic and all of which have mouth-parts of a very different type (Keilin, 1919; Madwar, 1937). Larvae of *Trichocera*, *Anisopus* and *Mycetobia* also differ from larvae of TIPULIDAE in many important characters. Thus, Tipulid larvae (De Meijere, 1916; Alexander, 1920) have incomplete head capsules which are partly retracted within the thorax (*i.e.*, they are hemicephalous). The respiratory system is metapneustic. The antennae have no bell-shaped sensory vesicle and are usually formed of an elongated segment bearing a group of digitiform sensory processes. The labrum is broad and is devoid of the two median ventral pads and of the pair of lateral comb-like sclerites (or " premandibles "). The mandibles are not divided into basal and distal pieces and have no medial expansion bearing opposed teeth. Usually a maxillary palp is well developed and is clearly circumscribed from the body of the maxilla. The labium is formed of a toothed mentum, made up of two plates, and of a prementum which is small and bears two small palpi which are not visible externally. Different genera of TIPULIDAE differ much in their internal anatomy. The herbivorous forms usually have four gastric caeca and a diverticulum arising from near the junction of the mid-gut with the hind-gut; and the salivary glands are long and coiled. In the carnivorous forms the gastric caeca may be reduced or absent, there is no diverticulum, and the salivary glands are elongated oval or cylindrical sacs.

On the other hand, larvae of *Trichocera*, *Anisopus* and *Mycetobia* have many features in common with larvae of SCATOPSIDAE; and with Psychodid larvae of the genus *Psychoda* (Keilin and Tate, 1937). In all of these genera the larva is eucephalous and the body is composed of three thoracic and eight abdominal segments; but Scatopsid larvae are peripneustic whereas larvae of *Trichocera*, *Anisopus*, *Mycetobia* and *Psychoda* are amphipneustic. In the structure of the mouth-parts larvae of *Trichocera*, *Anisopus*, *Mycetobia*, *Scatopse* and *Psychoda* all have the following features in common. There is a pair of comb-like sclerites on the ventral surface of the labrum. The mandibles are formed of a basal piece with a dentate process on its medial border, and a distal piece terminating in strong teeth and bearing fan-like groups of long, rigid setae. The maxillae are soft and fleshy and are divided into two lobes, an outer, the maxillary palp, bearing two groups of sensory papillae (" a " and " b "), and an inner lobe, the maxilla proper. The labium is reduced to a prementum bearing groups of sensory papillae which are visible externally and represent the labial palps. Larvae of *Scatopse* differ from the others in the absence of bell-shaped sensory vesicles on the antennae, but have another point in common with *Trichocera*, *Anisopus* and *Mycetobia* larvae in possessing sensory vestiges of the thoracic legs in the form of groups of 4 setae, 2 long and 2 short.

Whilst there is great divergency of opinion amongst systematists as to the relative value of adult and larval characters in the classification of Diptera, undoubtedly the correct attitude towards this question is that expressed by Edwards (1926 : 113) in the words : " We must conclude therefore that larval and adult characters should be treated as complementary to one another, and the evidence from each stage considered together. Sometimes the adults and sometimes the larvae will furnish the crucial points of the summing up; when the latter is the case, it may often be due to the fact that the affinities of the adults are obscured in a confusing complexity of secondary adaptations." From this standpoint future work on the taxonomy of the groups dealt with in the present paper should take into consideration the many structural characters held in common by larvae of *Trichocera*, *Anisopus*, *Mycetobia* and,

to a less degree, by *Olbiogaster*, and also the fact that a number of these characters are present in larvae of SCATOPSIDÆ and *Psychoda*. It is only by a careful consideration of both adult and larval characters that it can be determined whether or not the resemblances revealed by a study of the early stages indicate true phylogenetic relationship.

V. Summary.

The structure of the larvae and pupae of the genera *Trichocera*, *Anisopus*, *Mycetobia* and *Olbiogaster*, and of the pupa of *Mesochria*, is described in detail.

From a comparative study of the early stages of these genera it is concluded that *Trichocera*, *Anisopus*, *Mycetobia*, perhaps *Mesochria*, and, to a less degree, *Olbiogaster*, have many characters in common with each other.

Larvae of *Trichocera*, *Anisopus* and *Mycetobia* show marked differences in structure from larvae of TIPULIDAE and MYCETOPHILIDAE, but have many characters in common with larvae of SCATOPSIDAE and of *Psychoda* among the PSYCHODIDAE.

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Key to the Lettering of Figures.

a., sensory organ " a " of maxillary palp.
An., anus.
an., antenna.
an.s., anal shield.
b., sensory organ " b " of maxillary palp.
b.p., basal piece of mandible.
br., brain.
cm., comb-like sclerite of labrum (= " pre-mandible ").
d.l., dorsal lobe of labrum.
e.s., external scar.
f.b., fat body.
f.c., felt chamber.
f.l., fleshy lobe of maxilla.
h., hairs guarding entrance to pharynx.
h.f., fold of hypoderm.
h.g., hind-gut.
ht., heart.
hy., hypopharynx.
i.d.an., imaginal disc of antenna.
i.d.h., imaginal disc of head.
i.d.l., imaginal disc of leg.
i.s., internal scar.
l.p., labial palps.
lr., labrum.
md., mandible.
m.g., mid-gut.
m.p., maxillary palp.
mt., mentum.
mx., maxilla.
oe., oesophagus.
Ph., pharynx.
p.m., prementum of de Meijere (= labium).
pr., posterior ventral prominence of labrum.
r., rectum.
s.a., anterior spiracle.
s.d., salivary duct.
s.f., scar filament.
s.g., salivary gland.
s.p., postabdominal spiracles.
st.g., stomato-gastric ganglion.
t.h., thickened hypoderm.
tn., tentorial rods of head.
t.p., terminal, toothed, piece of mandible.
t.t., tracheal trunk.
v.g.l., first ganglion of ventral nerve chain.
v.g.2, second ganglion of ventral nerve chain.
v.h., ventral, or medial, teeth of mandible.